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The anterior temporal lobes and the functional architecture of semantic memory

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Abstract

Recently, three accounts have emerged on the role of the anterior temporal lobes (ATLs) in semantic memory. One account claims that the ATLs are domain-general semantic hubs, another claims that they underlie knowledge of unique entities specifically, and yet another account claims that they support social conceptual knowledge generally. Here, we review neuropsychological and neuroimaging studies that bear on these three accounts and offer suggestions for future research to elucidate the roles of the ATLs in semantic memory.

Keywords

Knowledge; Concepts; Lesion; fMRI; PET; Prosopagnosias

INTRODUCTION

There is widespread agreement that the neural architecture of semantic memory includes the anterior regions of the temporal lobes (ATLs). There is, however, little agreement on the precise role of the ATLs in semantic memory. Given the diverse anatomy and connectivity of this region—which includes the temporal pole, and the most anterior extents of the perirhinal and entorhinal cortices, and the anterior regions of the fusiform, inferior, middle, and superior temporal gyri—it is perhaps not surprising that assigning a single function to the ATL has remained elusive and controversial.

At present, three main theories have emerged on the bases of conflicting neuropsychological and functional imaging data. In one view, the ATLs serve as a semantic hub linking together conceptual information distributed throughout the brain (Lambon Ralph & Patterson, 2008; McClelland & Rogers, 2003; Patterson, Nestor, & Rogers, 2007), under another view the ATLs serve as a repository for knowledge of unique entities such as familiar people and landmarks (Damasio, Tranel, Grabowski, Adolphs, & Damasio, 2004; Tranel, 2006), and under a third view they function as a store for social conceptual information generally (Frith, 2007; Olson, Plotzker, & Ezzyat, 2007; Zahn et al., 2007, 2009). Although these accounts converge on a role for the ATLs in conceptual processing, they can be differentiated along three dimensions: (1) whether information in the ATL is domain-general or restricted primarily to a few conceptual categories, (2) whether that information pertains to broad classes of objects in a category or unique entities specifically, and (3) whether that information is represented locally within the ATL itself, or whether the region simply stores pointers or links to feature information stored in regions outside the ATLs. Here we briefly review the neuropsychological

and imaging data regarding the functions of the ATLs, and consider how these data bear on the semantic hub, unique entity, and social conceptual processing accounts.

Extensive behavioral, lesion, and functional imaging literatures demonstrate that conceptual knowledge arises from networks of brain regions distributed throughout the cortex for representing distinct object categories such as people, animals, and tools. The constituent regions within these networks each represent perceptual, motor, and affective properties experienced while interacting with category members (for a recent review, see Martin, 2007). An unanswered question, however, is whether there exists a central hub to link these property networks together. Recently, McClelland, Rogers, Patterson and colleagues have marshaled a compelling case that the brain must contain a central semantic hub to support generalizations across concepts that have similar conceptual relations but very different property profiles (Lambon Ralph & Patterson, 2008; McClelland & Rogers, 2003; Patterson et al., 2007; Rogers et al., 2004). For example, ostriches and alligators look and behave very differently, yet share many conceptual relations that humans can easily use to support categorical generalizations (e.g., both are animals, both live on land, both breathe air, both make a nice pair of boots, etc.). Semantic hub proponents argue that generalizations such as these can only be achieved in a model with a representational layer (a.k.a., a hub) that (1) stores abstract information about the similarity relations among categories, rather than property information *per se*; and (2) is domain-general, storing information for all categories (Patterson et al., 2007; for a detailed examination of parallel distributed processing/neural network models supporting this account, see Rogers & McClelland, 2004).

NEUROPSYCHOLOGICAL FINDINGS IN THE ANTERIOR TEMPORAL LOBES

Proponents of the hub account have almost universally asserted that the semantic hub is located in the ATLs, primarily on the bases of neuropsychological data from semantic dementia patients.¹ Semantic dementia, a subtype of frontotemporal dementia, is a degenerative disease associated with atrophic temporal lobes and broad semantic memory impairments in the presence of relatively intact functioning in other cognitive domains (Patterson et al., 2007). Semantic dementia patients' conceptual defects are more highly correlated with pathology in the lateral surface of the ATLs than medial temporal cortex (Levy, Bayley, & Squire, 2004). This finding is consistent with evidence that repetitive Transcranial Magnetic Stimulation (rTMS) over the lateral ATLs in healthy subjects temporarily slows object naming response speed (Pobric, Jefferies, & Lambon-Ralph, 2007).

There are reasons to be cautious, however, when interpreting both the rTMS and semantic dementia data. First, we know of no evidence that bombarding the anterior temporal region with 10 min of continuous stimulation before experimental tasks, as was done by Pobric and colleagues, produces a "virtual lesion" that is *specific* to the ATLs. To the contrary, this procedure alters neural activity in regions remote from the site of stimulation (e.g., Rounis et al., 2006). And with respect to semantic dementia patients, pathology is clearly not restricted to the anterior temporal lobes. Pathology often extends into the amygdala (Noppeney et al., 2007), and the frontal lobes (Brambati et al., 2009), and semantic memory impairments are equally correlated with pathology in the ATLs and posterior regions of the fusiform gyrus (Williams, Nestor, & Hodges, 2005). Furthermore, anterior temporal resection for intractable epilepsy does not invariably lead, and in fact rarely leads, to significant domain-general semantic memory impairments (Drane et al., 2008), although it is almost invariably associated with episodic memory deficits.²

¹It is important to note that the theoretical argument for why semantic memory requires a hub and the location of this hub in the brain are separate issues. One could accept the necessity for a hub, but argue for a different location.

In contrast to the global semantic impairments of semantic dementia patients, focal ATL damage has been associated with more selective semantic memory deficits. For example, anterior temporal resection can result in circumscribed impairments in recognizing and naming familiar/famous people, implicating the ATLs in the storage of person-specific information (Fukatsu, Fujii, Tsukiura, Yamadori, & Otsuki, 1999; Glosser, Salvucci, & Chiaravalloti, 2003; Tsukiura et al., 2003). Moreover, these patients also occasionally exhibit impaired recognition and naming of familiar/famous landmarks (Drane et al., 2008; Tranel, 2006), suggesting that the ATLs may store semantic information about unique entities specifically, rather than semantic memory generally. Finally, the left ATL may be important for the retrieval of proper names for people and landmarks (Tranel, 2006), and so serve as a convergence region linking conceptual knowledge about unique entities and entity-associated word (e.g., names), both of which are stored outside the ATLs (Damasio et al., 2004).

Proponents of ATL hub accounts generally offer two responses to the absence of gross semantic memory deficits following ATL resection and the relative specificity of unique entity deficits. First, they note that resected tissue is by definition unhealthy and that functional reorganization both pre- and postsurgery may mean the brains of long-term epilepsy patients are less than ideal models for normal brain-behavior relationships (Powell et al., 2007). Second, unlike semantic dementia, resections are unilateral, thus leaving a healthy, functioning hemisphere. This argument finds support in the observation that global semantic memory deficits are more pronounced when pathology is bilateral (Noppeney et al., 2007). Given these criticisms, functional neuroimaging data from healthy individuals engaged in conceptual tasks may be particularly useful.

FUNCTIONAL NEUROIMAGING FINDINGS IN THE ANTERIOR TEMPORAL LOBES

The vast majority of positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) studies of conceptual processing do not report activation in the ATLs. On the contrary, these studies largely implicate posterior ventral and lateral temporal cortices, as well as left inferior frontal cortex (Thompson-Schill, 2003). When ATL activations are reported in functional neuroimaging studies, it is usually when subjects are engaged in processing unique entities or performing social conceptual processing tasks.

Consistent with the unique entity account of ATL function, ATL activity has often been associated with viewing famous and familiar faces (Damasio et al., 2004; Grabowski et al., 2001; Gorno-Tempini et al., 1998; Leveroni et al., 2000; Nakamura et al., 2000; Pourtois, Schwartz, Segheir, Lazeyras, & Vuilleumier, 2005; Rotshtein, Henson, Treves, Driver, & Dolan, 2005; Sergent & Signoret, 1992; Sugiura et al., 2001; Tsukiura, Namiki, Fujii, & Iijima, 2003). The unique entity account gains yet more support from two PET studies reporting ATL activation when subjects viewed unique landmarks relative to unfamiliar locations (Grabowski et al., 2001; Nakamura et al., 2000). There are at least two reasons to be cautious, however, about extending the famous/familiar face findings to the representation of unique entities generally, rather than social knowledge specifically. First, Kriegeskorte, Formisano, Sorger, and Goebel (2007) using high-resolution fMRI and multivariate information-mapping analyses identified a region in the right inferior ATL carrying information that reliably discriminated among individual faces, but failed to observe ATL regions that discriminated among individual houses. Second, ATL activation does not require referencing information about specific, unique individuals. For example, ATL activation has often been reported when

²It is worth noting, however, that few detailed investigations of post-surgery semantic functioning in temporal lobe epilepsy have been published.

subjects infer the mental states and emotions of generic others in theory of mind tasks (for review, see Olson, Plotzker, & Ezzyat, 2007). Similarly, activity in the left ATL has been reported to correlate with deceit detection (Grezes, Frith, & Passingham, 2004), and the right ATL has been found to activate when subjects view photographs depicting scenes with moral connotations (e.g., physical assaults) *versus* similar nonmoral control scenes (Moll et al., 2002). More recently, Zahn and colleagues used both fMRI and PET imaging to show that activation of the right superior ATL was related to the representation of social abstract concepts such as *courage* or *generosity* (Zahn et al., 2007, 2009). Indeed, stimuli need not even be *explicitly* social to engage the ATLs. For example, the ATLs activate when subjects infer animacy and intentionality in the movements of abstract geometric shapes (Castelli, Happe, Frith, & Frith, 2000; Schultz et al., 2003). Taken together, these findings suggest that the ATLs might be engaged in social conceptual processing generally, rather than the representation of unique entities *per se*.

The inconsistency of ATL activations outside of social conceptual processing tasks is also curious in light of the semantic hub account. If the ATL is the hub of the human conceptual system, one might expect it to be consistently activated by conceptual processing tasks. Semantic hub proponents offer at least two explanations for this inconsistency. First, they point out that fMRI is currently the predominant imaging modality, and its image signal quality over the ATLs is relatively poor due to magnetic susceptibility artifacts (Devlin et al., 2000). To address this concern, hub proponents point to PET studies demonstrating ATL activations during a variety of conceptual processing tasks (Crinion, Lamon Ralph, Warburton, Howard, & Wise, 2003; Davis & Johnsrude, 2003; Devlin et al., 2000; Rogers et al., 2006; Vandenberghe, Nobre, & Price, 2002; Vandenberghe, Price, Wise, Josephs, & Frackowiak, 1996). Second, hub proponents have asserted that many imaging studies of conceptual processing fail to observe ATL activation because they require subjects to process stimuli at a level of specificity that is too general (Rogers et al., 2006; Tyler et al., 2004). As described earlier, semantic hub accounts claim that the ATL stores information about similarity relations among concepts. Rogers and colleagues (2006) hypothesized that the ATL should thus be more strongly activated by subordinate-level classification judgments of highly related concepts (e.g., differentiating among two different kinds of birds) than more general classifications (e.g., differentiating among animals and artifacts generally). In support of this hypothesis, they observed greater bilateral ATL activation when subjects made specific/subordinate-level classification judgments (blue jay *vs.* robin) than when they made basic-level (bird *vs.* dog) and superordinate (animal *vs.* vehicle) classification judgments. Even so, some studies do find ATL activation with basic-level concepts (e.g., Crinion et al. 2003; Devlin et al. 2000; Vandenberghe et al. 1996).

Rogers et al. (2006) unfortunately did not directly compare ATL activation for social and nonsocial stimuli, so it is difficult to know how their findings relate to the other theories of ATL functioning. In fact, none of the imaging studies that support a general semantic hub account of the ATL directly compare social and nonsocial stimuli.

CONCLUSIONS AND RECOMMENDATIONS

Although the domain-general semantic hub account of ATL functioning has gained much attention recently, the neuro-psychological and imaging data supporting it remain sparse and not without complications. In contrast, social conceptual processing, and particularly knowledge of famous and familiar individuals, has been consistently implicated in the deficits of ATL lesion patients and activation patterns of healthy adults undergoing functional neuroimaging. More work remains, however, if we are to more precisely understand the ATL's information content. We offer the following recommendations as a guide to future studies of the ATL's contribution to conceptual knowledge representation.

First, much could be learned from studies directly comparing the domain-general semantic hub account with the unique entity and social conceptual processing accounts. In general, evidence for these three accounts has evolved in parallel literatures, with little effort to directly test these accounts against each other. In fact, at present only one study has directly compared the domain-general semantic hub and social conceptual processing accounts, with the results strongly supporting the latter (Simmons, Reddish, Bellgowan, & Martin, in press).

Second, although there is much to implicate the ATLs in the processing of social conceptual knowledge generally, there also remain good reasons to think that the region is dedicated to the storage of information about unique entities. In light of this, it will be important for future research to directly test these two accounts. It is also worth noting, however, that the accounts are not necessarily mutually exclusive. A potentially integrative account could be that the ATLs store information about unique entities, with a relative bias toward social unique entities. This makes sense in light of the fact that only two of the three possible patterns of deficits have been reported among patients with famous/familiar person- and landmark-knowledge deficits. As described earlier, patients most commonly present with intact landmark-knowledge, but deficient person-knowledge. Less frequently they present with deficits for both categories. There have been no reports, however, of intact person-knowledge in the presence of landmark deficits.

A more speculative possibility is that distinct subregions exist in the anterior temporal lobes for person- and place-unique entities, thus recapitulating the topographic distinction observed in posterior ventral temporal cortex, with place information represented medially in the parahippocampal cortex and face information represented laterally in the fusiform gyrus (see Grill-Spector, 2003, for review). Importantly, such micro-organization in ATL functional anatomy would be almost impossible to isolate in lesion patients, smoothed away in lower-resolution PET data, and obscured in fMRI by signal artifacts that are worse over anteromedial regions. In light of these limitations, perhaps the only means currently available to identify functional micro-organization in the ATLs is direct cortical stimulation and/or recordings.

Finally, although more neuropsychological patient data are always welcome, theories of ATL function may benefit from research using new functional imaging methodologies to map the ATL's information-selectivity and functional connectivity. For example, multi-voxel pattern analyses are somewhat less susceptible to signal degradation in the ATL than traditional univariate fMRI analyses (Mur, Bandettini, & Kriegeskorte, 2009) and may be a powerful tool for determining whether population codes across the region carry information discriminating among social- and nonsocial stimuli. In addition, knowing the regions to which the ATL structures are most strongly connected should help clarify its role within the wider conceptual system. This calls for better characterizations of the ATL's functional connectivity profile, and how its connectivity is altered during various task contexts.

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